EFFECTS OF BROWSING BY NATIVE UNGULATES ON THE SHRUBS IN BIG SAGEBRUSH COMMUNITIES IN YELLOWSTONE NATIONAL PARK

Francis J. Singer[1] and Roy A. Renkin[2]

ABSTRACT.—The effects of elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) browsing on shrubs in big sagebrush (*Artemisia tridentata*) communities were monitored over a 31-year period in Yellowstone National Park. Ungulates were restricting Wyoming big sagebrush (spp. *wyomingensis*) heights, size, and recruitment on the lower-elevation stratum only, while no such suppression was observed on the high-elevation stratum. Parallel increases in mountain big sagebrush (spp. *vaseyana*) densities and cover occurred over the study period on both browsed and unbrowsed sites at the higher-elevation stratum, although big sagebrush, green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) were slightly taller and crown sizes were slightly larger on unbrowsed than browsed sites. Wyoming big sagebrush utilization (percent leader use) was eight times higher ($\bar{x} = 87 \pm 7.2\%$ by pronghorns, mule deer, and elk) on the low-elevation winter range stratum (the Boundary Line Area [BLA] portion of the winter range), while mostly mountain big sagebrush with leader use averaged only $11 \pm 4.1\%$ (nearly all by elk) on the high-elevation range stratum. In addition, annual aboveground biomass production of big sagebrush did not differ between browsed and unbrowsed study sites on the high-elevation stratum of the winter range. Population turnover was higher on browsed big sagebrush at the high-elevation plots; seedling germination and survival rates were higher on browsed plots versus unbrowsed plots. No difference was observed in percent dieback of big sagebrush adult plants between browsed and unbrowsed plots at the higher stratum. Browsing did not influence the number of leaves or seedstalks per plant ($P > .05$), but leaves averaged 45% longer and seedstalks 42% longer on browsed big sagebrush. Ungulate browsing, however, apparently suppressed production, germination, and survival of Wyoming big sagebrush on the low-elevation stratum. Numbers of Wyoming big sagebrush declined 43% and cover declined 29%, 1957–1990, on browsed sites on the BLA. Annual biomass production on browsed sites at the low-elevation stratum was only 6–35% that of unbrowsed sites, and big sagebrush recruitment was less on browsed sites. Percent leader use of big sagebrush did not differ between the period of ungulate reductions, 1962–1969, and the 1980s on the lower stratum ($\bar{x} = 87\%$ leader use), but utilization was less on higher portions of the winter range during the period of elk reductions ($\bar{x} = 2\%$) than during the 1980s following cessation of elk controls ($\bar{x} = 11\%$).

Key words: big sagebrush browsing, northern Yellowstone elk, pronghorn, mule deer, Cervus elaphus.

Native populations of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) were artificially reduced in Yellowstone National Park (YNP), particularly from 1942 through 1967 (Meagher 1973, Houston 1982). Reductions were terminated in 1967 when an experimental management program of natural regulation was initiated (Cole 1971, Houston 1976, 1982). Elk and other ungulate numbers tripled after cessation of controls, and concerns were expressed over high ungulate densities (Chase 1986, Kay 1991). Appropriate numbers of ungulates for the park are unknown since no similar control area exists where wolves (*Canis lupus*) are present and where ungulate migrations are completely unrestricted by humans (Cayot et al. 1979, Peek 1980). Ungulate densities are likely slightly above natural conditions, in that three independent computer

models suggest 8–15% fewer elk and 10–25% fewer bison would occupy the system if wolves were recovered (Garton et al. 1990, Boyce 1993, Mack and Singer 1993).

Early workers expressed concern about apparent overbrowsing and declines in big sagebrush (*Artemisia tridentata*) due to possible overabundant populations of elk and pronghorn. As early as the 1930s, Rush (1932) and Cahalane (1943) reported losses of big sagebrush over lower-elevation areas of the northern winter range. Rush (1932) reported that less-palatable rabbitbrushes (*Chrysothamnus* spp.) were increasing. Kittams (1950) concluded that big sagebrush numbers were declining at both lower and higher elevations of the northern winter range. He felt that physical disturbances of big sagebrush by elk during cold periods (shattering and trampling) and an

absence of big sagebrush reproduction contributed to the decline. Declines in big sagebrush at the lower-elevation Boundary Line Area (BLA) were attributed by Kittams (1950) to excessive levels of browsing by pronghorn. Park management established a goal to reduce the pronghorn herd by 50% (Kittams 1959); by 1969 pronghorn numbers were artificially reduced from 600–800 to less than 200 through a combination of artificial reductions and severe winters (Barmore 1980).

Houston (1982) provided alternative interpretations concerning big sagebrush. He reported increases in big sagebrush numbers over all the northern winter range except the BLA near Gardiner, MT, where numbers declined. Houston (1982) compared photos taken during the 1860s to photos retaken in the 1970s. He attributed the increase in big sagebrush at higher elevations to fire suppression and the decline in big sagebrush in the BLA to a return to more natural conditions following the removal of intense grazing by livestock in the early 1930s when the area was added to the park. In 1986 the U.S. Congress directed the National Park Service (NPS) to conduct a study to evaluate whether native ungulates were overgrazing the northern winter range (Congressional Record 1986).

Our objectives were to document trends in big sagebrush abundance on a series of permanently marked plots from 1958 to 1990. Height, canopy size, twig lengths, and annual production of shrubs were compared between browsed and unbrowsed sites.

STUDY AREA

Shrub sampling was conducted on unbrowsed (exclosed) and paired browsed sites at eight ungulate exclosures erected in 1958 and 1962 on Yellowstone's northern winter range. The eight exclosures, 2 ha in size, were located on gently rolling upland steppe ridge and the intervening swale habitats (Fig. 1). We divided the study area into a low-elevation stratum (the BLA of Houston 1982) with two exclosures, and a much larger, high-elevation stratum (n = 6 exclosures), based on large differences in ungulate species, elevation, snowpack, precipitation, and big sagebrush subspecies (Fig. 1).

Underlying soils are typic calciborolls, aridic haploborolls, and aridic calciborolls (Lane

1990). Precipitation averages 30 cm at the low-elevation exclosures and 55 cm at the high-stratum exclosures (Houston 1982, Despain 1991). The northern winter range is approximately 1100 km^2 and is located along the upper Yellowstone River drainage. Elevations range from 1500 m at the low-stratum exclosures to about 2200 m at the highest exclosure. The northern winter range is lower, warmer, and drier than the remaining higher plateaus of YNP (Houston 1982). As a result, 80% of the ungulates in the park during winter are found on the northern winter range (Singer 1991).

Dominant shrubs at all the study sites include two subspecies of big sagebrush at the high-elevation stratum, nearly all mountain big sagebrush (*A. t. vaseyana*) with some basin big sagebrush (*Artemisia tridentata tridentata*), while Wyoming big sagebrush (*A. t. wyomingensis*) occurs in the low-stratum study sites. The big sagebrush subspecies vary markedly in their site requirements, growth, and preferences by ungulates (Beetle 1960, Welch et al. 1981, Beetle and Johnson 1982, McArthur and Welch 1982). Rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) are found at all study sites. *Grayia spinosa* and *Atriplex canescens* occur at the low-stratum study sites (Houston 1982). Dominant grasses are bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria pyramidata*), bluegrasses (*Poa compressa, P. sandbergii,* or *P. pratensis*), and thick-spike wheatgrass (*A. dasystachyum*; Houston 1982, Wambolt et al. 1987, Despain 1991).

Pronghorn and mule deer occupy only the low-elevation stratum of approximately 52 km^2 within Yellowstone National Park (Barmore 1980, Houston 1982, Singer 1991). About one-half of the pronghorn population also summers in the low-elevation stratum. The lower-elevation (about 1500 m) exclosures are located in typical, nearly snow-free, rolling xeric shrub and mixed grassland habitats. Elk occupy both strata and the entire winter range of 810–1000 km^2 (Houston 1982, Singer 1991). Only elk and bison winter near the high-elevation stratum exclosure sites. Winter snow depths near the higher exclosures (1639–2200 m) are typically 0.4–0.6 m, which are excessive for pronghorn and deer. The abrupt elevation rise for Mt. Everts separates the high and low strata.
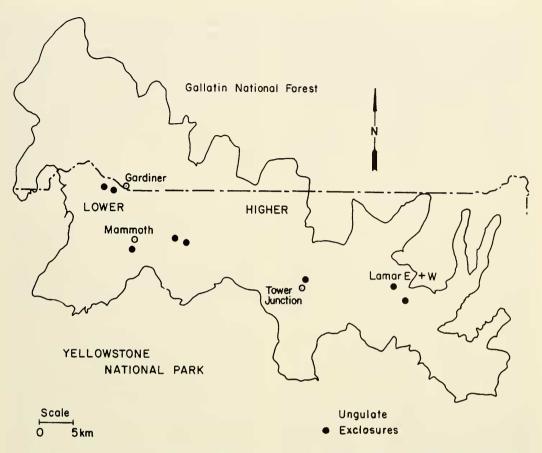
Fig. 1. Map of the northern Yellowstone ungulate winter range and the high-elevation stratum (six exclosures) and low-elevation stratum (two exclosures) big sagebrush study sites. Pronghorn, mule deer, and the Wyoming subspecies of big sagebrush were found only at the low-elevation stratum.

The bison winter range expanded from about 130 km² in the 1960s in the higher stratum to about 460 km² in the late 1980s during a period of bison population and range expansion (Meagher 1989, Singer and Norland 1995). Periodic bison use of the low-elevation stratum occurred following the population expansion in the late 1980s (Meagher 1989), but vegetation measures reported here are nearly all prior to any bison use of the low-elevation stratum.

Elk numbered about 8000 in 1958–1962 when initial monitoring of the sagebrush belt transects began. Elk were subsequently further reduced by artificial controls to less than 5000 in 1967 (Houston 1982). After cessation of controls, elk steadily increased, with counts ranging from 16,000 to 19,000 from 1982 to 1989 (Singer et al. 1989, Singer 1991). Bison were also artificially controlled until 1967. After cessation of controls, bison on the northern range increased from less than 100 in 1967 to 850 by

1988 (Houston 1982, Meagher 1989). Pronghorn were artificially reduced from 600–800 to <200 (Barmore 1980), and pronghorn numbers remained <200 until about 1981. During the 1980s—apparently due to milder winters—pronghorn increased to about 600 (Singer 1991). Mule deer counts increased from 1000 in 1985 to 2300 in 1988 over the entire deer winter range, the majority of which lies north of the park boundary (Singer 1991). Conversely, mule deer counts just within the park boundaries declined from 230 in the 1960s (Barmore 1980) to about 100 in 1988, in spite of the overall herd increase.

METHODS

Ungulate Densities and Diets

Average ungulate densities near the exclosures were based on actual aerial counts made from fixed-wing aircraft as described in

Barmore (1980), Houston (1982), Meagher (1989), Singer (1991), and Singer and Norland (1995). Densities are uncorrected for visibility bias (Samuel et al. 1988) and therefore represent minimum average densities for the study periods—undoubtedly some animals were missed on the counts (Singer et al. 1989). Diets of all four ungulates found near the study sites on the northern winter range were estimated for each of three winters, December–March 1985–1988, from microhistological analysis of fecal samples (Washington State University, Wildlife Habitat Laboratory, Pullman). Each sample was a composite of 5 g of fresh dung material from 6–12 dung piles. Aggregate average percentages are reported for significant species and plant groups. To avoid confusion between similar species, fresh samples were collected for groups of animals immediately after the groups had vacated an area. Bighorn sheep (*Ovis canadensis*) use steeper terrain on the northern range, and moose (*Alces alces*) are found at higher elevations; neither species was observed near the study sites.

Shrub Utilization Rates

Winter ungulate herbivory rates were sampled on the browsed transects in late winter–spring before leaf emergence (usually late April) in 1963–1969, 1987, 1989, and 1990. Percent twig utilization was obtained from counts of all browsed and unbrowsed twigs on each shrub located in the transect. Diameters at basal point and browsing point were measured on 20 random shoots on every fifth browsed shrub of each species, and bite sizes were estimated following Pitt and Schwab (1990).

Trends in Big Sagebrush, 1958–1990

Five exclosures were erected in 1957 and three more in 1962 ($n = 8$ total). The exclosures were placed in sites representative of mixed big sagebrush/bunchgrass communities. Paired belt transects (each 1.5 m × 30.5 m = 46.5 m^2) were permanently located inside and outside eight of the exclosures (one per exclosure treatment) in big sagebrush communities (Canfield 1941, Parker 1954). Each matched pair of transects was as nearly comparable as possible in terms of slope, aspect, elevation, shrub species, and shrub cover (Barmore 1980, Houston 1982); nevertheless, differences might have occurred. Sampling of transects occurred

at the date of exclosure, which should reveal any initial site differences. The transect for exclosure was selected arbitrarily. Heights and species of all shrubs found on the belt transects were recorded in 1958, 1962, 1967, 1974, 1981, 1986, and 1990. Numbers of individual shrubs and any shrub seedlings were tallied. Aerial cover of all shrubs was mapped on graph paper, and shrub cover was later estimated using a grid (Barmore 1980, Houston 1982).

Detailed Site Comparisons in 1986 and 1987

Shrub belt transects were not replicated at a site ($n = 1$ transect per treatment per location, 13 transects total) and were useful primarily for long-term trends and assessment of pretreatment conditions (Parker 1954). In 1986 and 1987 more intensive and better replicated measurements ($n = 15$ plots per treatment) were gathered; 15 circular plots, each 1.7 m in radius (9.3 m^2), were randomly located in big sagebrush stands both inside and outside six exclosures. The tallest height, widest diameter, and perpendicular diameter were recorded for each shrub within each plot. The number of totally dead shrubs was recorded. The percentage of dead material on partially live shrubs was estimated. At every fifth shrub of each species, lengths and diameters of 10 randomly sampled twigs were measured, and every vegetative twig and reproductive stalk were counted. A minimum of 100 twigs of each species from each site was collected, dried, and weighed. Canopy area for each individual shrub was estimated following Peek (1970) from the formula for the area of an ellipse:

$$\text{area} = \left(\frac{\pi}{4}\right) d^1 d^2,$$

where d^1 = largest diameter and d^2 = its perpendicular diameter. All plots and long-term transects were located more than 25 m from exclosure fences to avoid the effects of snowdrifts or ungulate trails along the fences.

Mean shrub height, largest crown area, shoot numbers and lengths, and total shrub cover were compared using a two-way ANOVA, with browsing and exclosure location as treatments. The six exclosures should be considered replications of one treatment (browsing) with 5 d.f. used to test for differences among the treatment and replications. Replications at a location

included the 15 random plots in each treatment (15 × 2 × 8 locations = 240 plots of 9.3 m²). Nonparametric procedures were used for percent twig utilization comparisons between the 1960s and 1980s and for other data that were nonnormal or with unequal variances (F-max tests; Sokal and Rohlf 1981). Frequency distributions of shrubs in browsed and unbrowsed plots were compared using the Kolomogorov-Smirnov test (Zar 1974). All differences discussed are significant at the P < .05 level unless otherwise indicated.

Aboveground biomass production of shrubs was estimated from the numbers of shrubs per plot times the average number of reproductive and vegetative shoots per plant times the average dry weight of shoots. Regression equations for dry weight of shoots (independent variable) were calculated following MacCracken and Viereck (1990) from diameters at base (dependent variable) and length (dependent variable) of shoots. Separate regression equations were calculated for reproductive and vegetative shoots of big sagebrush, green rabbitbrush, and rubber rabbitbrush. The regressions on dry weight were applied to the sample of all twig diameters and lengths to estimate average twig biomass.

RESULTS

Ungulate Densities and Diets

Ungulate densities approximately doubled during the study period on the low-elevation stratum (Table 1), whereas they approximately tripled on the high-elevation stratum during the same period (Table 1). Pronghorn consumed 81% shrubs in their diet, followed by mule deer 50%, elk 8%, and bison 1% (Table 2). Pronghorn diets were 49% big sagebrush, mule deer consumed 23%, and elk diets were only 4%. The higher combined ungulate densities and the presence of pronghorn and mule deer, both of which eat more big sagebrush, suggest that ungulate herbivory on big sagebrush will be greater on the low-elevation stratum study sites. Since pronghorn consume 12x more big sagebrush in their diets than elk and 2x more than mule deer, and since pronghorns also spend summers in the low-elevation stratum, we suspect pronghorn were the most important herbivore on big sagebrush on the low-elevation stratum.

TABLE 1. Average minimum densities of elk, pronghorn, mule deer, and bison near the lower- and higher-elevation exclosures on the northern winter range of Yellowstone National Park. Reported densities are based upon actual counts from fixed-wing aircraft (Houston 1982, Meagher 1989, Singer 1991) and are uncorrected for visibility bias.

| | Ungulate density (no./km²) | |
Ungulate	Lower exclosures	Higher exclosures
1965–1968		
Elk	6	6
Pronghorn	3	0
Mule deer	4	0
Bison	0	1
Total	13	7
1985–1988		
Elk	16-19	16-19
Pronghorn	7-10	0
Mule deer	2	0
Bison	tr	2
Total	25-31	18-21

Shrub Utilization Rates

Big sagebrush utilization rates were consistently high (87%) and did not differ between 1963–1969 and 1985–1988 at the low-elevation stratum study sites dominated by the more palatable (to pronghorn) Wyoming big sagebrush (Table 3, Mann-Whitney U tests, P > .05). Pronghorn and elk reductions during 1962–1967 apparently did not result in any decrease in percent leader use of Wyoming big sagebrush on the low stratum. Green rabbitbrush was also used heavily at the low-stratum sites where deer and pronghorn occurred (Table 3). Utilization rates of big sagebrush at the higher sites dominated by mostly mountain big sagebrush, however, increased about sixfold after ungulates increased threefold (Table 3, P < .05). Use of green rabbitbrush did not increase significantly at the high stratum during this period of ungulate increase. Percent leader use of big sagebrush at the lower-elevation sites averaged 87%, but leader use averaged only 11% at the higher sites. Bite sizes averaged 73% of vegetative shoots and 83% of reproductive shoots (n = 180 measured diameters of browsed shoots and 540 unbrowsed vegetative and reproductive shoots). Consumption of annual aboveground biomass of big sagebrush by ungulates averaged about 68% at the low-elevation stratum sites and 9% at higher-elevation stratum sites.

TABLE 2. Mean percent of shrubs in winter diets of four ungulates on Yellowstone's northern winter range, 1985–1988, determined by microhistological analysis of feces ($\bar{x} \pm$ SE).

Ungulate (no. aggregate samples)	Big sagebrush		Rabbit- brush[a]		Eurotia lanata		Fringed sage		Total shrubs[b]	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Elk (28)	3.8	3.1	1.6	2.7	0.4	1.0	1.0	2.0	7.8	4.1
Bison (25)	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.6
Mule deer (21)	23.2	15.1	7.2	4.6	0.7	1.0	17.9	16.7	49.7	20.9
Pronghorn (20)	48.7	18.0	5.3	3.5	5.8	6.0	18.5	13.7	80.5	15.7

[a]Rabbitbrush includes *Chrysothamnus nauseosus* and *C. visidiflorus*.
[b]Total shrubs also includes *Populus* spp., *Salix* spp., and *Atriplex* spp.

Big Sagebrush Trends in Densities, Heights, and Cover, 1958–1990

Big sagebrush on belt transects in the lower stratum differed at the time of exclosure in 1958–1962. Densities were similar, but average heights were 50% and cover about 60% those values on transects selected for exclosure (Table 4). Big sagebrush densities, heights, and cover, however, were similar between browsed and unbrowsed transects at the time of exclosure on the high-elevation stratum.

Apparently, ungulates were suppressing Wyoming big sagebrush on the low-elevation stratum during the study period. Wyoming big sagebrush densities decreased 43% and big sagebrush cover decreased 29% on the low-stratum browsed site over the 31-year period (Table 4). Density and cover of Wyoming big sagebrush increased dramatically (350% and 830%, respectively) in the unbrowsed sites of the low stratum. Big sagebrush individuals were taller on unbrowsed sites (Table 4).

Herbivory effects were less on the high-elevation stratum study sites, and all trends were similar for browsed and unbrowsed sites. Mountain and basin big sagebrush density declined, and canopy cover increased on both browsed and unbrowsed belt transects, 1958–1990 (Table 4). Wyoming and basin big sagebrush density declined 39%, but cover increased 39% on browsed sites over the 31 years. Heights of big sagebrush increased on both browsed and unbrowsed sites, but more on unbrowsed sites (Table 4).

Detailed Site Comparisons of Densities, Cover, and Biomass Production in 1986 and 1987

Densities of big sagebrush ($F = 50.9$), total canopy cover of big sagebrush ($F = 8.1$), individual shrub crown area ($F = 22.5$), and heights of big sagebrush ($F = 79.8$, $P < .05$) differed between a much larger sample of browsed ($n = 15$) and unbrowsed plots ($n = 15$ per location, $n = 180$ total) sampled in 1986 and 1987. In each case, however, location was also significant, and the interaction between location and browsing was significant. For example, sagebrush individuals were 59% taller on unbrowsed plots at six exclosure sites, but at the Blacktail exclosures sagebrush plants were taller on browsed plots. Heights of big sagebrush, green rabbitbrush, and horsebrush increased with elevation in both treatments. As a consequence of this exploratory analysis and significant interactions with location, our division of plots into a high and low strata appeared justified, and we analyzed data from the lower and higher study sites separately in all subsequent analyses.

Big sagebrush individuals were shorter and crowns smaller in browsed versus unbrowsed

TABLE 3. Percent of twigs browsed in big sagebrush communities on Yellowstone's northern range. Total ungulate numbers increased twofold at the lower exclosures and threefold at the higher exclosures between 1963–1969 and 1985–1988. The same transects of 46.5 m² each ($n = 5$) were sampled both periods; only these five browsed transects were sampled 1963–1969.

Location Shrub species (n = transects)	1963–1969		1985–1988	
	$\bar{x}$	SE	$\bar{x}$	SE
Low elevation ($n = 2$)				
Big sagebrush	88.0	4.2	86.8	7.2
Green rabbitbrush[a]			70.1	10.5
Spiny hopsage[a]			14.8	4.3
High elevations ($n = 3$)				
Big sagebrush	1.9	0.8	11.6	3.5*
Green rabbitbrush	6.7	3.6	8.9	2.9
Horsebrush			46.6	11.4

[a]Only big sagebrush utilization was sampled 1963–1969, and green rabbitbrush at only the higher exclosures.
*$P < .05$, according to Mann-Whitney U tests.

TABLE 4. Changes in density, heights, and canopy cover of individual big sagebrush shrubs between time of exclosure placement in 1958 and 1990 on permanently marked 46.5 m² shrub transects, Yellowstone's northern winter range.

| Treatment | Density of shrubs | | | | Heights (cm) | | | | Canopy cover (m²/46.5 m²) | | | |
| | 1958-1962 | | 1990 | | 1958-1962 | | 1990 | | 1958-1962 | | 1990 | |
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lower exclosures[a]												
Browsed	21	7	12	2	0.7	0.3	0.5	0.1	19	4	16	4
Unbrowsed	23	15	103	27	1.8	0.6	16.7	0.9	28	7	50	9
Higher exclosures[b]												
Browsed	67	18	41	1.7	1.9	0.9	5.9	1.6	12	2	42	7
Unbrowsed	72	34	37.8	6.2	1.6	0.2	8.6	0.9	10	2	82	9

[a]Big sagebrush subspecies in these transects, mostly *A. t. wyomingensis*, are apparently highly palatable to pronghorns.
[b]Big sagebrush subspecies include mostly *A. t. vaseyana*.

exclosure sites at low elevations ($F = 29.8$, 14.3, respectively), but there was no difference in heights or crown sizes due to browsing at the high-elevation sites ($P > .05$, Table 5). Horsebrush was shorter and crowns were smaller on browsed and unbrowsed exclosure sites at the higher elevations only ($F = 14.5$, 4.6, Table 5). Common rabbitbrush was shorter on browsed plots at the lower elevations, but it was taller on browsed plots at the higher-elevation exclosure sites (Table 5). Density of Wyoming big sagebrush was less on browsed versus unbrowsed plots at the lower exclosures ($F = 14.7$), but there was no effect of browsing at the higher exclosures (Table 6). No difference in the number of dead big sagebrush individuals was observed between browsed and unbrowsed plots at either elevation category ($P > .05$). Twenty-two times more seedlings of the year were observed on browsed than unbrowsed plots at higher elevations ($F = 2.7$, Table 6).

Big sagebrush contributed 82–99% of annual aboveground shrub production in these shrub communities. Browsing did not consistently influence the production of big sagebrush or green rabbitbrush at higher exclosure sites, but browsed rubber rabbitbrush produced less biomass at higher-elevation sites (Table 6). Both Wyoming big sagebrush and rubber rabbitbrush produced much less aboveground biomass on browsed sites on the low study sites (Table 6).

There was no influence from browsing on the number of vegetative or reproductive shoots per shrub for big sagebrush or green rabbitbrush. Reproductive shoots averaged 42% longer (Friedman test, $\chi_r^2 = 38$, $n = 6$ locations, $P < .05$), and vegetative shoots averaged 45% longer on browsed versus unbrowsed big sagebrush (Friedman test, $\chi_r^2 = 42$, $n = 6$ locations, $P < .05$, Table 7). There was no effect of browsing on length of reproductive shoots of green rabbitbrush ($P > .05$).

DISCUSSION

Other studies indicate mountain big sagebrush is preferred and eaten at a higher rate by mule deer and elk than Wyoming big sagebrush, while basin big sagebrush is the least preferred (Sheehy and Winward 1981, Welch et al. 1981, Personius et al. 1987). Our observations initially appear in contrast with this generalization; we observed 70% more winter utilization on Wyoming big sagebrush than mountain big sagebrush. Too few basin big sagebrush occurred on the study sites to draw any conclusions. Our data do not constitute a palatability test, however, in that mountain and Wyoming subspecies did not occur at the same study sites. We suspect pronghorn were the primary herbivore on Wyoming big sagebrush in lower study sites; pronghorn find the Wyoming subspecies highly palatable (Beetle 1960, Beetle and Johnson 1982), and that subspecies was more available to all ungulates due to shallow snows and more winds in the low stratum. Ungulate preference for big sagebrush subspecies also varies between locales (Welch et al. 1981, McArthur and Welch 1982); for example, Dietz and Nagy (1976) found Wyoming big sagebrush was preferred by mule deer in Colorado.

Mountain and basin big sagebrush seedling germination, establishment, and survival were apparently enhanced by browsing and ungulate grazing (possibly due to secondary effects

Table 5. Individual shrub crown and heights of shrubs in browsed and unbrowsed (protected) sites on Yellowstone's northern elk winter range. Samples were drawn from ($n = 180$) plots of 9.3 m^2 each located randomly in browsed and unbrowsed sites in 1986 and 1987.

	Crown area (cm^2)				Heights (cm)			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
Shrub species								
Location	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big sagebrush[a]								
Lower (Artrwy)	678	85	347	66*	50	2	37	4*
Higher	798	90	524	51	79	3	71	2
Horsebrush								
Lower	45	7	37	13	15	1	11	2
Higher	575	222	71	93*	63	10	27	3*
Common rabbitbrush								
Lower	287	109	278	85	78	8	43	3*
Higher	196	42	881	590*	59	5	50	11
Green rabbitbrush								
Lower	76	13	104	55	36	11	28	3
Higher	742	70	392	42	79	3	53	2*

*Significant difference between grazed and control means using ANOVA, $P < .05$.
[a]Big sagebrush subspecies included lower exclosures—*A. t. wyomingensis* only; higher exclosures—mixed populations of *A. t. tridentata* and *A. t. vaseyana*, but nearly all *A. t. vaseyana*.

Table 6. Estimated annual production (g/m^2) of the most common shrubs in browsed and unbrowsed big sagebrush communities at six exclosures on Yellowstone's northern winter range ($n = 15$ plots each in both browsed and unbrowsed treatments at each site). Wyoming big sagebrush is found only at the lower-stratum exclosures, and mixed populations of nearly all mountain with some basin big sagebrush at the higher exclosures.

| | Lower elevations | | | | | Higher elevations | | | |
| | Unbrowsed | | Browsed | | | Unbrowsed | | Browsed | |
Exclosure location	$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Estimated biomass (g/m^2)									
Big sagebrush	18		1.9			73.6		72.6	
Green rabbitbrush	0.1		1.5			3.1		5.8	
Common rabbitbrush	0.6		0.3			5.9		4.1	
No. big sagebrush individuals/9.3 m^2									
No. alive	16	2	2	1*		13	2	15	2
No. dead	1.3	0.4	0.6	0.5		3.3	0.8	5.9	1.9
No. seedlings	0.8	0.3	0.2	0.1		0.2	0.1	4.4	1.4*

*$P < .05$ according to t tests. No tests were conducted on biomass since it was estimated from a product of no. of plants × average no. of shoots × average weight of shoots. Tests were conducted on each of those parameters separately, however (see text and Table 7), suggesting statistically significant differences at the lower elevations.

such as reductions of herbaceous vegetation competition and ungulate hoof action) at the higher winter range, but the opposite trend was observed on lower sites. McArthur et al. (1988) also observed more big sagebrush seedlings on a site browsed by mule deer in winter than on an unbrowsed site. The physical act of ungulate grazing, with its accompanying hoof action, greater soil disturbance, more bare ground, and less standing dead vegetation and litter, may provide conditions more suitable to big sagebrush germination. Big sagebrush individuals are smaller on browsed sites, which may also benefit establishment and survival of seedlings due to reduced competition for light, soil moisture, and other resources.

Ungulate herbivory suppressed big sagebrush on the lower-elevation sites, where almost no recruitment of Wyoming big sagebrush occurred on browsed sites; apparently few seedlings survive the intense browsing. Wyoming big sagebrush reproduces more successfully

TABLE 7. Numbers and lengths of reproductive and vegetative stalks on shrubs in browsed and unbrowsed plots in big sagebrush communities on Yellowstone's northern range (n = no. shrubs).

Species Location	No. reproductive flowers/shrub				Length (cm) of flower stalks			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big sagebrush								
Lower (Wyoming spp. only)	15	6	13	10	4	0.2	8	0.6**
Higher (basin and mountain spp.)	21	7	17	6	14	0.7	18	0.6**
Green rabbitbrush								
Higher	10	3	16	10	11	0.4	12	0.4
	No. vegetative shoots/shrub				Length (cm) of vegetative shoots			
Big sagebrush								
Lower	99	23	88	18	2	0.1	3	0.4
Higher	83	31	59	12	5	0.5	7	0.5**
Green rabbitbrush								
Higher	33	7	52	20	6	0.2	8	0.4**

*$P < .05$.
**$P < .01$. Differences between numbers in browsed and unbrowsed plots were tested with t tests and lengths with Mann-Whitney U tests.

than the other subspecies on xeric sites (Welch and Jacobson 1988), and the xeric, sodic clay soils of the low stratum are clearly more suitable to Wyoming big sagebrush. At the high levels of ungulate herbivory we observed (roughly 68% biomass removal), the Wyoming subspecies is presently suppressed by ungulates.

The ability of Wyoming big sagebrush to recover from herbivory is less than for mountain and basin big sagebrush. Wyoming big sagebrush is shorter (individuals often do not exceed 0.3 m), seedling growth rates are lower, and current annual growth is less than for the other two subspecies (McArthur and Welch 1982, Booth et al. 1990). The approximately 66% decline in numbers of mule deer using the lower stratum within the park over the past two decades may be due to the localized Wyoming big sagebrush decline. Pronghorn did not decline in the lower stratum during the same period, but pronghorn, unlike mule deer, were artificially reduced well below carrying capacity levels during the 1960s (Houston 1982), and they may still be recovering from the reductions.

Increases in height and cover of big sagebrush are reported after protection from ungulates. Robertson et al. (1970) reported big sagebrush cover increased 76% after 30 years of protection from browsing, although mean heights declined 12%. Heights and crown sizes were similar, but live cover by big sagebrush was greater on unbrowsed sites on a mule deer winter range, primarily due to a greater dieback of browsed big sagebrush (McArthur et al. 1988). Average crown dieback was 64% in the browsed area and 17% in the unbrowsed area (McArthur et al. 1988). Mule deer use was heavy (370 deer-use days/ha), and dieback of big sagebrush occurred after two successive winters of heavy snowfall (McArthur et al. 1988).

Browsing by native ungulates stimulated seedstalks and leaves of big sagebrush and leaves of green rabbitbrush on the study sites. Stagnation of shrubs occurred inside big game exclosures after only two years of exclosure—nonuse of big sagebrush resulted in an average 36% reduction in biomass production over clipped plants (Tueller and Tower 1979). Numbers of sprouts of green rabbitbrush were similarly increased by clipping (30% herbage removal), and new growth was longer, leaves were larger, and leaves remained green for one month longer (Willard and McKell 1978). On the other hand, browsing of more than 80% of the leaders of mountain big sagebrush by mule deer resulted in a reduction of 50–93% in total number of seedstalks per plant and a reduction of 0–53% in length of seedstalks (Wagstaff and Welch 1991). Grazed grasses on the northern Yellowstone winter range have higher protein levels (Coughenour 1991), and grazing stimulates aboveground growth of grasses (Frank and McNaughton 1993). Increased vigor in new growth of browsed shrubs on the Yellowstone northern winter

range is consistent with these observations of grasses, and shrub vigor may be the result of increased rates of nutrient cycling due to ungulate defecation and urination (McNaughton 1979). In addition, plant competition is reduced and water availability may be increased on browsed sites on the northern winter range due to smaller crown sizes and fewer transpiring tissues for individual shrubs.

Historic mean duration between fires was 25 years on the Yellowstone northern winter range, but due to fewer fire starts and active fire suppression, no significant burning of grasslands occurred between 1870 and 1988 (Houston 1973, Romme and Despain 1989). Big sagebrush communities had not yet achieved climax postfire state on the northern winter range as indicated by increases in heights and cover of both browsed and unbrowsed big sagebrush individuals between 1958 and 1990. Browsed big sagebrush communities on higher-elevation ranges were replacing themselves; many successful seedlings and small individuals were observed on browsed versus unbrowsed sites. Lomasson (1948) observed almost no reproduction for 40 years in a stand of big sagebrush, but then reproduction increased as the original population began dying. Average life span of big sagebrush is 53–72 years, and in a mature, undisturbed stand, most big sagebrush individuals are in the 55–59-year age class (Roughton 1972). Sagebrush recovery following fire varies from a few years to 30 years depending upon environmental conditions for reestablishment (Sneva 1972, Harniss and Murray 1973). If most big sagebrush communities we studied on the northern winter range last burned in the 1840–1890 period (Houston 1973), then most big sagebrush populations should have approached senescence and population turnover at the time of the 1986–87 sampling.

Ungulate herbivory levels on the lower study stratum restricted growth, establishment, and survival of big sagebrush at the time of this investigation, although browsed big sagebrush communities were stable or increasing at the higher elevation. Suppression of growth and reproduction of plants by increasing native ungulates can result in a new, altered plant-ungulate equilibrium (Sinclair 1977, Caughley 1981). If unnatural (human-caused) concentrations of ungulates cause plant alterations, the situation is not accept-

able under NPS policy (U.S. Department of the Interior 1988). Houston (1982) concluded densities of ungulates in the BLA were unnatural and artificially high due to animal avoidance of hunting outside the park. If so, some form of ungulate management—control, encouragement of migrations—is justified on the BLA. Elk and pronghorn reductions in the 1960s, however, did not reduce percent leader use or improve the declining status of big sagebrush in the BLA. Either effective ungulate densities remained the same near the big sagebrush study sites, the ungulate reductions did not go on long enough, or high preference for the Wyoming subspecies by pronghorn maintained high levels of herbivory in the area during the control period.

We caution that we were unable to calculate appropriate or recommended ungulate herbivory levels or ungulate densities for the northern winter range. Our data included two dichotomous periods in ungulate management. The first period of our study, 1958–1968, was clearly a period of ungulate underpopulation during which time elk, bison, and pronghorn were controlled far below ecological carrying capacity (ECC) densities (Barmore 1980, Houston 1982, Boyce 1993, Mack and Singer 1993, Singer and Norland 1995). The second period of our investigations, 1986–1988, likely was a time of ungulate densities in excess of natural conditions, at least for elk and bison. This statement is not based upon any comparisons to control conditions (no similar ecosystem exists with wolves and nondisrupted migrations for a comparison), but upon the conclusions of Houston (1982) that elk concentrations were unnaturally high in the low-elevation BLA stratum, and computer predictions that elk and bison would number 8–25% less following wolf restoration (Garton et al. 1990, Boyce 1993, Mack and Singer 1993). Pronghorn densities in relation to ECC are unknown—one author feels coyotes (Canis latrans) are suppressing pronghorn on the northern Yellowstone winter range and that, following wolf restoration, coyotes will decline and pronghorn will further increase (Berger 1991). Wolf restoration occurred on the study area during the winter of 1994–95, providing an opportunity to test the effects of wolves upon ungulate-plant interactions in the Yellowstone ecosystem (Cook 1993).

LITERATURE CITED

BARMORE, W. J. 1980. Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone Park. Unpublished report, Yellowstone National Park files, Mammoth, WY.

BEETLE, A. A. 1960. A study of sagebrush: the section *Tridentata* of *Artemisia*. University of Wyoming, Agricultural Experiment Station Bulletin 368. 68 pp.

BEETLE, A. A., AND K. L. JOHNSON. 1982. Sagebrush in Wyoming. Wyoming Agricultural Experiment Station Bulletin. 68 pp.

BERGER, J. 1991. Greater Yellowstone's ungulates: myths and realities. Conservation Biology 5: 353–363.

BOOTH, G. D., B. L. WELCH, AND T. L. C. JACOBSON. 1990. Seedling growth rates of 3 subspecies of big sagebrush. Journal of Range Management 43: 432–436.

BOYCE, M. S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor, Ecological issues on reintroducing wolves into Yellowstone National Park. U.S. National Park Service Science Monograph 22. Denver, CO.

CAHALANE, V. H. 1943. Elk management and herd regulation—Yellowstone National Park. Transactions of the North American Wildlife Conference 8: 95–101.

CANFIELD, R. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388–394.

CAUGHLEY, G. 1981. Overpopulation. Pages 7–19 *in* P. A. Jewell, S. H. Holt, and D. Hart, editors, Problems in management of locally abundant wild animals. Academic Press, New York. 361 pp.

CAYOT, L. J., J. PRUKOP, AND D. R. SMITH. 1979. Zootic climax vegetation and natural regulation. Wildlife Society Bulletin 7: 162–169.

CHASE, A. 1986. Playing God in Yellowstone. Atlantic Monthly Press, Boston. 446 pp.

COLE, G. F. 1971. An ecological rationale for the natural or artificial regulation of ungulates. Transactions of the North American Wildlife Conference 36: 417–425.

CONGRESSIONAL RECORD. 1986. Senate S.12613. U.S. House of Representatives.

COOK, R. S., EDITOR. 1993. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph 22. Denver, CO.

COUGHENOUR, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28: 71–82.

DESPAIN, D. G. 1991. Yellowstone vegetation, consequences of environment and history in a natural setting. Roberts Rinehart Publishing, Boulder, CO. 239 pp.

DIETZ, D. R. AND J. G. NAGY. 1976. Mule deer nutrition and plant utilization. Pages 71–78 *in* C. W. Workman and J. B. Low, editors, Mule deer decline in the West—a symposium. Utah State University, College of Natural Resources, Logan. 134 pp.

FRANK, D., AND S. J. MCNAUGHTON. 1993. Interactive ecology of plants, large mammalian herbivores and drought in Yellowstone National Park. Unpublished doctoral dissertation, Syracuse University, Syracuse, NY. 150 pp.

GARTON, E. O., R. L. CRABTREE, B. B. ACKERMAN, AND G. WRIGHT. 1990. The potential impact of a reintroduced wolf population on the northern Yellowstone elk herd. Pages 3–59 *in* Yellowstone National Park, U.S. Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Study Team, University of Minnesota Cooperative Park Studies Unit, editors, Wolves for Yellowstone? Report to the United States Congress. Volume II. Research and analysis.

HARNISS, R. O., AND R. B. MURRAY. 1973. Thirty years of vegetation change following burning in sagebrush-grassland range. Journal of Range Management 26: 322–325.

HOUSTON, D. B. 1973. Wildfires in northern Yellowstone National Park. Ecology 54: 1111–1117.

———. 1976. Research on ungulates in northern Yellowstone National Park. Pages 11–27 *in* Research in the parks. Transactions of the National Park Symposium, National Park Service Symposium No. 1.

———. 1982. The northern Yellowstone elk: ecology and management. Macmillan Publishing Co., Inc., New York. 474 pp.

KAY, C. E. 1991. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Unpublished doctoral dissertation, Utah State University, Logan. 490 pp.

KITTAMS, W. H. 1950. Sagebrush on the lower Yellowstone range as an indicator of wildlife stocking. Yellowstone National Park files, Mammoth, WY. 14 pp.

———. 1959. Future of the Yellowstone wapiti. Naturalist 10: 30–39.

LANE, J. 1990. Characterization and comparison of soils inside and outside of grazing exclosures on Yellowstone National Park's northern winter range. Unpublished master's thesis, Montana State University, Bozeman.

LOMASSON, T. 1948. Succession in sagebrush. Journal of Range Management 1: 19–21.

MACCRACKEN, J. G., AND L. A. VIERECK. 1990. Browse regrowth and use by moose after fire in interior Alaska. Northwest Science 64: 11–18.

MACK, J. A., AND F. J. SINGER. 1993. Using Pop-II models to predict effects of wolf predation and hunter harvests on elk, mule deer, and moose on the northern range. Pages 49–74 *in* R. S. Cook, editor, Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph 22. Denver, CO.

MCARTHUR, E. D., AND B. L. WELCH. 1982. Growth rate differences among big sagebrush (*Artemisia tridentata*) accessions and subspecies. Journal of Range Management 35: 396–401.

McArthur, E. D., A. C. Blauer, and S. C. Sanderson. 1988. Mule deer induced mortality of mountain big sagebrush. Journal of Range Management 41: 114–117.

McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113: 691–703.

Meagher, M. M. 1973. The bison of Yellowstone National Park. National Park Service Science Monograph Series 1. 161 pp.

———. 1989. Range expansion by bison of Yellowstone National Park. Journal of Mammalogy 70: 670–675.

Parker, K. W. 1954. A method for measuring trend in range condition on National Forest ranges with supplemental information for measurement of vigor, composition, and browse. USDA Forest Service Report. 37 pp.

Peek, J. M. 1970. Relation of canopy area and volume to production of three woody species. Ecology 51: 1098–1101.

———. 1980. Natural regulation of ungulates. Wildlife Society Bulletin 8: 217–227.

Personius, T. L., C. L. Wambolt, J. R. Stephens, and R. G. Kelsey. 1987. Crude terpenoid influence on mule deer preference for sagebrush browse. Journal of Range Management 40: 84–88.

Pitt, M. D., and F. E. Schwab. 1990. Assessment of a nondestructive method for estimating browse use. Journal of Wildlife Management 54: 175–179.

Robertson, J. H., D. L. Neal, R. McAdams, and P. T. Tueller. 1970. Changes in crested wheatgrass ranges under different grazing treatments. Journal of Range Management 23: 27–34.

Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39: 695–699.

Roughton, R. D. 1972. Shrub age structure on a mule deer winter range in Colorado. Ecology 53: 615–625.

Rush, W. M. 1932. Northern Yellowstone elk study. Montana Fish and Game Commission, Helena. 131 pp.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1988. Visibility bias during aerial surveys of elk in north-central Idaho. Journal of Wildlife Management 51: 622–630.

Sheehy, D. P., and A. H. Winward. 1981. Relative palatability of seven Artemisia taxa to mule deer and sheep. Journal of Range Management 34: 397–399.

Singer, F. J. 1991. The ungulate prey base for wolves in Yellowstone National Park. Pages 323–348 in R. B. Keiter and M. S. Boyce, editors, The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, CT.

Singer, F. J., and J. Norland. 1995. Niche relationships within a guild of ungulates following release from artificial controls, Yellowstone National Park, Wyoming. Canadian Journal of Zoology 72: In press.

Singer, F. J., W. Schreier, J. Oppenheim, and E. O. Garton. 1989. Drought, fires, and large mammals. Bioscience 39: 716–722.

Sinclair, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. University of Chicago Press, Chicago, IL. 355 pp.

Sneva, F. A. 1972. Grazing return following sagebrush control in eastern Oregon. Journal of Range Management 25: 174–178.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco, CA.

Tueller, P. J., and J. D. Tower. 1979. Vegetation stagnation in three-phase big game exclosures. Journal of Range Management 32: 258–263.

U.S. Department of Interior, National Park Service. 1988. Management policies. U.S. Government Printing Office, Washington, DC.

Wagstaff, F. J., and B. L. Welch. 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal of Range Management 44: 72–74.

Wambolt, C. L., R. G. Kelsey, T. L. Personius, K. D. Striby, A. F. McNeal, and K. M. Havstad. 1987. Preference and digestibility of three big sagebrush subspecies and black sagebrush as related to crude terpenoid chemistry. Pages 71–73 in F. D. Provenza, J. T. Flinders, and E. D. McArthur, compilers, Symposium on plant-herbivore interactions. USDA Forest Service, General Technical Report INT-222. Ogden, UT.

Welch, B. L., and T. L. C. Jacobson. 1988. Root growth of Artemisia tridentata. Journal of Range Management 41: 332–334.

Welch, B. L., E. D. McArthur, and J. N. Davis. 1981. Differential preferences of wintering mule deer for accessions of big sagebrush and black sagebrush. Journal of Range Management 34: 409–411.

Willard, E. E., and C. M. McKell. 1978. Response of shrubs to simulated browsing. Journal of Wildlife Management 42: 514–519.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ. 620 pp.